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The holoplanktonic Mollusca from the southern Gulf of Mexico. Part 1: heteropods

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Abstract: This study documents the vertical and horizontal distribution of the heteropod Mollusks in the neritic epipelagic layer of the southern Gulf of Mexico. Plankton samples were taken at 28 sampling stations below the 18°N parallel in the southernmost Gulf of Mexico, during May and November 1995. Five vertical strata (0-6, 6-12, 12-18, 45-55 and 95-105 m) were sampled with an opening-closing net system equipped with 75-cm diameter and 505-µm mesh size nets, and a total of 187 samples were collected. Fourteen species of heteropod Mollusks were identified, and the dominant species, accounting for the 97% of the total abundance, were *Atlanta lesueurii* (60%), *A. gaudichaudi* (15%), *Firoloida desmarestia* (12%) and *A. selvagensis* (10%). In the vertical plane, their highest densities were recorded in the 0-18 m upper layer. Seasonally, only *A. gaudichaudi* registered its highest abundance in November. We hypothesize that shifts in seasonal dominance of heteropod species is an ecological strategy to avoid competition for feeding resources. The carinariid *Carinaria challengeri* was registered for the first time in the western Atlantic. A detailed documentation of the worldwide distribution of the 14 heteropod species is included.

Résumé : *Les mollusques holoplanctoniques de la partie méridionale du Golfe du Mexique. 1ère partie : hétéropodes.* Cette étude documente la distribution verticale et horizontale des Mollusques hétéropodes dans la zone épipélagique néritique du sud du Golfe du Mexique. Les échantillons de plancton ont été prélevés à 28 stations au sud du parallèle 18°N, la zone la plus méridionale du Golfe du Mexique, durant les mois de mai et novembre 1995. 187 échantillons ont été récoltés à cinq intervalles de profondeur de la colonne d'eau (0-6, 6-12, 12-18, 45-55 et 95-105 m) avec un filet ouvrant-fermant de 75 cm de diamètre et 505 µm de vide de maille. Quatorze espèces de Mollusques hétéropodes ont été identifiées ; les espèces dominantes, expliquant 97% de l'abondance totale, étaient *Atlanta lesueurii* (60%), *A. gaudichaudi* (15%), *Firoloida desmarestia* (12%) et *A. selvagensis* (10%). Dans la colonne d'eau, leurs densités plus élevées ont été enregistrées dans la couche de 0-18 m. Saisonnièrement, seule *A. gaudichaudi* a enregistré son abondance la plus élevée en novembre. Nous suggérons que les variations saisonnières de dominance des espèces d'hétéropodes pourraient être une stratégie écologique permettant d'éviter la compétition pour les ressources alimentaires. Le carinariidé *Carinaria challengeri* est signalé pour la première fois en Atlantique occidental. Nous donnons également une documentation détaillée sur la distribution mondiale des 14 espèces d'hétéropodes identifiées dans cette étude.

Keywords: species richness ● Mollusks ● Vertical distribution ● Epipelagic zone ● Worldwide distribution

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Introduction

Heteropods are gastropod mollusks that live in the Atlantic, Pacific and Indian Oceans, mainly at tropical and subtropical latitudes (Tesch, 1949; Lalli & Gilmer, 1989). They can be grouped into three families. In the Atlantidae, the calcareous transparent shell contains the entire animal; in the Carinariidae, the shell is much smaller than the animal and only covers the whole or a small part of the visceral nucleus; and, in the Pterotracheidae, the shell is lacking (Tesch, 1949; Thiriot-Quiévreux, 1973).

Heteropods are mainly found in the epipelagic zone, but some species can inhabit mesopelagic waters (Pafort-van Iersel, 1983; Lalli & Gilmer, 1989). Horizontally, heteropods are affected by proximity to land masses, temperature and salinity conditions, and the flow patterns of ocean currents (Xu, 2007; Seapy, 2008). Also, their position in the water column may be affected by the availability of food, degree of turbulence, and light intensity (Sanvicente-Añorve et al., 2013). Despite their gelatinous structure, heteropods can be active swimmers; speed and locomotion efficiency increase in the larger species. Swimming is not a continuous activity, instead, they swim to capture their prey or when avoiding predators. When disturbed, the body is capable of rapid flexion, allowing both locomotion and rapid change of direction (Tesch, 1949; Lalli & Gilmer, 1989).

The primary source of food of heteropods is gelatinous zooplankton (Lalli & Gilmer, 1989). Some species are opportunistic predators, feeding on a wide range of prey that mainly includes salps, doliolids and chaetognats (Seapy, 1980), whereas other heteropod species prefer siphonopores or other planktonic mollusks (Hamner et al., 1975; Lalli & Gilmer, 1989). Interestingly, copepods are non-preferred prey, which may be due to the difficulty of digesting the exoskeleton and/or the time-consuming processes of mastication (Seapy, 1980). Well-developed eyes in heteropods are a good indicator that these organisms are visual predators. The shape of the retina is like a long, narrow ribbon, allowing a restricted field of view of 0-180° long and only few degrees high (Land, 1982). To solve this problem, al least one heteropod species is able to make systematic scanning movements of the eyes through a 90° arc to create a composite image and detect their prey in the surrounding water, even at night (Land, 1982).

In the Gulf of Mexico, scientific literature concerning the heteropods is very scarce. Taylor & Berner (1970) examined the heteropod fauna collected in oceanic waters of the Gulf, and Castellanos & Suárez-Morales (2001) studied the distribution and abundance of the Carinariidae and Pterotracheidae in neritic and oceanic waters of the southern Gulf. To better understand the biodiversity of the heteropod fauna, in this study we analyze the composition and vertical distribution of these organisms in the epipelagic layer of neritic waters from the southern Gulf of Mexico. We also gave documentation on their worldwide distribution.

Material and Methods

All plankton samples used in this study were collected in neritic waters of the southern Gulf of Mexico in May and November 1995. The sampling grid included 28 oceanographic stations located between 18-20 °N and 91-95 °W (Fig. 1). Each tow was oblique through each of the targeted depth intervals (0-6, 6-12, 12-18, 45-55 and 95-105 m) and a total of 187 samples were collected using a multiple opening-closing net equipped with 75-cm diameter and 505-µm mesh size nets. The volume of water filtered by each net was determined using flow meters. Salinity and temperature were measured at each station with a CTD probe. All samples were preserved in 4% buffered seawater-formalin solution. In the laboratory, specialized literature (Pafort-van Iersel, 1983; Richter & Seapy, 1999; Janssen, 2012) was used to determinate the specimens and their abundance data were expressed as individuals per 100 m^3 (ind.100 m^{-3}). The significance of two estimated heteropod densities was tested using the Mann-Whitney *U* test. Day/night mean densities were

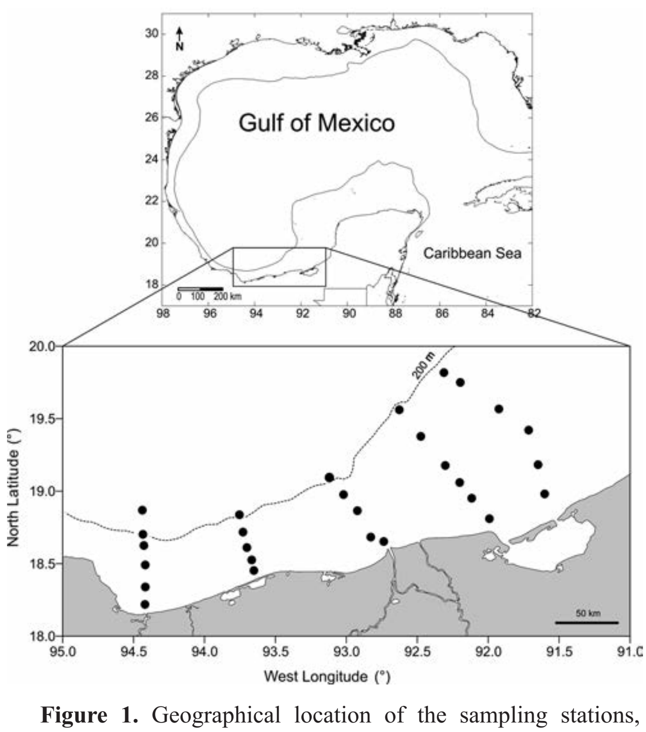

Figure 1. Geographical location of the sampling stations, southern Gulf of Mexico.

compared using only the data of the 0-18 m upper layer of stations over the shelf border to avoid the influence of lagoonal and riverine outflows. This work constitutes the first of two parts of a research considering the whole holoplanktonic mollusca in the southern Gulf of Mexico.

Results

Fourteen species of heteropod mollusks belonging to six genera and three families were recorded in neritic waters of the southern Gulf of Mexico during May and November 1995 (Table 1). The most diverse family was Atlantidae, represented by eight species. Four species dominated the heteropod fauna in the studied region: *Atlanta lesueurii* (60.25% of the total abundance), *A. gaudichaudi* (14.58%), *Firoloida desmarestia* (11.92%) and *A. selvagensis* (9.98%). In the horizontal plane, all the four species had a wide distribution in neritic waters of the southern Gulf. Interestingly, *A. selvagensis* was absent from coastal zones of low salinity (< 35). The remaining ten species were scarce and accounted only for the 3.27% of the total abundance.

Seasonally, *A. lesueurii*, *Firoloida desmarestia* and *A. selvagensis* was more abundant in May ($p < 0.05$); *A. gaudichaudi* was more abundant in November, but no significant differences ($p > 0.05$) between the two months were detected. Comparisons of densities between day and night periods revealed that *F. desmarestia* was significantly ($p < 0.05$) more abundant during the daytime in the upper 0-18 m strata in both months (Table 2), whereas *A. gaudichaudi* and *A. selvagensis* were most abundant ($p < 0.05$) at night in May and November, respectively. *Atlanta lesueurii* did not show diel significant differences ($p > 0.05$).

Information of the water column stratum where the species were recorded, as well as a detailed worldwide distribution of the 14 species here encountered is presented below. While documenting species distribution, we considered four zonal categories: tropical (0 to 30°, both latitudes), subtropical (30 to 60°), polar (60 to 90°) and cosmopolitan (all latitudes). In the search of the distributional records of species we included some synonymies and/or invalid names. A summary of the worldwide distribution of heteropod species, as well as detailed notes on their taxonomy, anatomy and ecological aspects are found in the Tree of Life webpages by Seapy (2009).

Clade Littorinimorpha Golikov & Starobogatov, 1975

Superfamily Pterotracheoidea Rafinesque, 1814

(= 'Heteropoda')

Family Atlantidae Rang, 1829

Atlanta brunnea Gray, 1850

Table 1. Mean densities (ind 100 m^{-3}) of heteropod species at five strata (m) of the water column during two seasons. Number of samples in parentheses.

Species	MAY					NOVEMBER					%
	0 - 6 (28)	6 - 12 (27)	12 - (16)	45 - 55 (11)	95 - 105 (11)	0 - 6 (28)	6 - 12 (28)	12 - 18 (17)	45 - 55 (11)	95 - 105 (10)	
Clade Littorinimorpha											
Atlantidae											
Atlanta brunnea	0.00	0.01	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.04
Atlanta gaudichaudi	0.89	0.98	0.41	0.28	0.21	2.74	3.85	3.70	0.35	0.33	14.58
Atlanta inclinata	0.02	0.03	0.04	0.05	0.08	0.00	0.00	0.00	0.03	0.06	0.31
Atlanta lesueurii	27.66	22.28	5.01	0.97	0.43	0.04	0.04	0.02	0.06	0.20	60.25
Atlanta peronii	0.00	0.00	0.21	0.13	0.08	0.02	0.01	0.00	0.00	0.03	0.50
Atlanta selvagensis	3.14	3.09	1.28	0.12	0.23	0.33	1.08	0.13	0.00	0.00	9.98
Atlanta tokiokai	0.00	0.08	0.11	0.17	0.16	0.00	0.00	0.00	0.00	0.00	0.54
Oxygyrus inflatus	0.04	0.18	0.53	0.07	0.00	0.00	0.01	0.00	0.00	0.00	0.89
Carinariidae											
Cardiapoda placenta	0.00	0.04	0.00	0.02	0.05	0.00	0.01	0.02	0.06	0.00	0.22
Carinaria challengeri	0.00	0.00	0.00	0.05	0.04	0.00	0.00	0.00	0.00	0.00	0.09
Carinaria lamarckii	0.00	0.00	0.24	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.28
Pterotracheidae											
Firoloida desmarestia	0.88	2.36	3.62	1.78	0.53	0.38	0.74	0.53	0.41	0.00	11.92
Pterotrachea coronata	0.00	0.00	0.00	0.00	0.02	0.00	0.03	0.18	0.00	0.14	0.39
Pterotrachea hippocampus	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.05	0.00	0.09

Table 2. Day and night mean densities (ind 100 m^{-3}) of four heteropod species during two seasons. Dawn and dusk (6-7 am/pm) data were eliminated for calculations. Number of samples in parentheses. * significant differences between day and night.

Species	MAY		NOVEMBER	
	day (21)	nigth (9)	day (17)	nigth (12)
Atlanta lesueurii	3.52 ± 6.00	0.16 ± 0.25	0.02 ± 0.12	0.00 ± 0.00
Atlanta gaudichaudi	0.24 ± 0.64	2.13 ± 2.89*	1.07 ± 2.73	0.21 ± 0.38
Firoloida desmarestia	4.18 ± 5.68	0.56 ± 0.52*	1.21 ± 2.33	0.30 ± 0.34*
Atlanta selvagensis	1.49 ± 2.38	0.42 ± 0.47	0.33 ± 0.52	0.05 ± 0.14*

Material examined

3 specimens.

Water column stratum

6-12 m.

Distribution

Circumglobal at tropical and subtropical latitudes. Western Atlantic: United States (Florida, Texas); Bermuda, Greater Antilles (Cuba, Haiti, Puerto Rico), Lesser Antilles (Aruba, Bonaire, Curacao); Sargasso Sea, throughout the Gulf of Mexico. Eastern Atlantic: Azores, Selvagens, Cape Verde Islands. Eastern Mediterranean Sea. Indian Ocean: Red Sea. Central Pacific: United States (Hawaii). Eastern Pacific: Mexico (18ºN), Costa Rica, Ecuador, Peru (15ºS) (Tesch, 1949; Odé & Speers, 1967; Taylor & Berner, 1970; Michel & Foyo, 1976; Echelman & Fishelson, 1990; Skoglund, 1992; Lyons, 1998; Rolán, 2005; de Vera et al., 2006; Seapy, 2008; Suárez-Morales et al., 2009; Frias-Martins, 2010; Miloslavich et al., 2010; Janssen, 2012).

Remarks

The worldwide distribution here presented is based on the records of *A. brunnea* and *A. fusca*.

Atlanta gaudichaudi Gray, 1850

Material examined

689 specimens.

Water column stratum

0 -105 m.

Distribution

Circumglobal at tropical and subtropical latitudes. Western Atlantic: United States (New Jersey, Maryland, Texas); Greater Antilles (Cuba); Sargasso Sea, central and eastern Gulf of Mexico. Eastern Atlantic: Selvagens Islands. Indian Ocean: Mozambique; Madagascar, western Australia. Eastern Pacific: United States (California), Mexico (west coast of the Baja California Peninsula, Gulf of California), Costa Rica, Colombia, Ecuador, Peru (della-Croce & Frontier, 1966; McGowan, 1967; Odé & Speers, 1967; Taylor & Berner, 1970; Frontier, 1973; Vecchione & Grant, 1983; Skoglund, 1992; Cediel-Parra et al., 1995; Seapy et al., 2003; de Vera et al., 2006; Ayón et al., 2008; Suárez-Morales et al., 2009; Jennings et al., 2010; Miloslavich et al., 2010; Angulo-Campillo et al., 2011).

Atlanta inclinata Gray, 1850

Material examined

12 specimens.

Water column stratum

0-105 m.

Distribution

Circumglobal at tropical and subtropical latitudes. Western Atlantic: United States (New Jersey, Maryland, Florida, Texas), Mexico (Quintana Roo), Argentina (Patagonian shelf); Greater Antilles (Cuba, Jamaica, Puerto Rico); Sargasso Sea, throughout the Gulf of Mexico. Eastern Atlantic: Senegal; Cape Verde Islands. Mediterranean Sea: Italy. Indo-Western Pacific: China; Madagascar, Australia. Central Pacific: United States (Hawaii). Eastern Pacific: United States (California), Mexico (west coast of the Baja California Peninsula, Gulf of California), Costa Rica, Peru (Frontier, 1963; McGowan, 1967; Odé & Speers, 1967; Taylor & Berner, 1970; Michel & Foyo, 1976; Vecchione & Grant, 1983; Seapy, 1990; Diouf, 1991; Michel & Michel, 1991; González, 1998; Lyons, 1998; Seapy et al., 2003; Rolán, 2005; Vasilyev, 2004; Xu, 2007; Ayón et al., 2008; Oliverio, 2008; Suárez-Morales et al., 2009; Jennings et al., 2010; Miloslavich et al., 2010; Angulo-Campillo et al., 2011).

Atlanta lesueurii Gray, 1850

Material examined

2280 specimens.

Water column stratum

0-105 m.

Distribution

Circumglobal at tropical and subtropical latitudes. Western Atlantic: United States (Texas, Florida); throughout the Gulf of Mexico. Eastern Atlantic: Cape Verde Islands; north-eastern Atlantic (between 30 and 50°N). Mediterranean Sea. Indo-Western Pacific: China; Chagos Archipelago, Seychelles, Australia. Central Pacific: United States (Hawaii). Eastern Pacific: United States (California), Mexico (west coast of the Baja California Peninsula), Costa Rica, Colombia, Peru (Tesch, 1910; Dales, 1957; McGowan, 1967; Odé & Speers, 1967; Taylor & Berner, 1970; Skoglund, 1992; Cediel-Parra et al., 1995; Lyons, 1998; Seapy et al., 2003; Rolán, 2005; Xu, 2007; Ayón et al., 2008; Oliverio, 2008; Seapy, 2008; Suárez-Morales et al., 2009; Janssen, 2012).

Remarks

Geographical records of the species correspond to *A. lesueuri* and *A. lesueurii.*

Atlanta peronii Lesueur, 1817

Material examined

17 specimens.

Water column stratum

0-105 m.

Distribution

Circumglobal at tropical and subtropical latitudes. Western Atlantic: United States (New Jersey, Maryland, Florida, Texas), Mexico (Tamaulipas, Veracruz, Campeche, Quintana Roo), Colombia, Venezuela, Brazil; Greater Antilles (Cuba, Jamaica, Haiti, Dominican Republic, Puerto Rico), Lesser Antilles (Virgin Islands, Aruba, Curacao, Bonaire); Sargasso Sea, throughout the Gulf of Mexico. Eastern Atlantic: Scotland, Ireland; Azores, Selvagens, Cape Verde Islands. Eastern Mediterranean Sea. Indo-Western Pacific: Chagos Archipelago, Seychelles, Australia. Central Pacific: United States (Hawaii), French Polynesia. Eastern Pacific: United States (Oregon, California), Mexico (west coast of the Baja California Peninsula), Costa Rica, Colombia, Peru (Tesch, 1910; Dales, 1957; Rice & Kornicker, 1965; McGowan, 1967; Odé & Speers, 1967; Taylor & Berner, 1970; Michel & Foyo, 1976; Vecchione & Grant, 1983; Michel & Michel, 1991; Skoglund, 1992; Rios, 1994; Cediel-Parra et al., 1995; Pérez-Rodríguez, 1997; González, 1998; Lyons, 1998; Seapy et al., 2003; Rolán, 2005; Çevik et al., 2006; de Vera et al., 2006; Ayón et al., 2008; Seapy, 2008; Suárez-Morales et al., 2009; Tröndlé & Boutet, 2009; Frias-Martins, 2010; Jennings et al., 2010; Miloslavich et al., 2010; Janssen, 2012).

Remarks

Distributional records correspond to *A. peroni* and *A. peronii.*

Atlanta selvagensis de Vera & Seapy, 2006

Material examined

377 specimens.

Water column stratum

0-105 m.

Distribution

Tropical. Western Atlantic: Panama; Gulf of Mexico. Eastern Atlantic: Azores, Selvagens Islands. Eastern Mediterranean Sea. Indian Ocean (Taylor & Berner, 1970; Michel & Foyo, 1976; de Vera & Seapy, 2006; de Vera et al., 2006; Janssen & Seapy, 2009; Frias-Martins, 2010; Janssen, 2012).

Remarks

This species was described by de Vera & Seapy (2006) and recognized as a valid species by Janssen & Seapy (2009). Owing to morphological similarities, previous studies confounded *A. selvagensis* with *A. inflata* and considered the second species to occur in all the oceans. However, in an excellent revision of museums' materials and historical documents, Janssen & Seapy (2009) concluded that *A. inflata* only occurs in the Pacific Ocean, whereas *A. selvagensis* distributed in the Atlantic and Indian oceans.

Atlanta tokiokai van der Spoel & Troost, 1972

Material examined

21 specimens.

Water column stratum

6-105 m.

Distribution

Tropical. Western Atlantic: southwestern Caribbean Sea. Indian Ocean: western Australia. Central Pacific: United States (Hawaii). Eastern Pacific: United States (California) to Peru, Mexico (Gulf of California), Costa Rica (van der Spoel & Troost, 1972; Skoglund, 1992; Seapy et al., 2003; Seapy, 2008; Suárez-Morales et al., 2009; Angulo-Campillo et al., 2011).

Oxygyrus inflatus Benson, 1835

Material examined

25 specimens.

Water column stratum

0-55 m.

Distribution

Circumglobal at tropical and subtropical latitudes. Western Atlantic: from United States (Massachusetts, Florida, Texas) to Brazil; Bermuda, Bahamas; Sargasso Sea, throughout the Gulf of Mexico. Eastern Atlantic: Cape Verde Islands. Eastern Mediterranean Sea. Indo-Western Pacific. Central Pacific: United States (Hawaii). Eastern Pacific: United States (California), Costa Rica, Panama, Peru (Maury, 1922; Tesch, 1949; Odé & Speers, 1967; Taylor & Berner, 1970; Abbott, 1974; Michel & Michel, 1991; Lyons, 1998; Seapy et al., 2003; Rolán, 2005; Xu, 2007; Ayón et al., 2008; Seapy, 2008; Suárez-Morales et al., 2009; Jennings et al., 2010; Janssen, 2012).

Remarks

The worldwide distribution here presented corresponds to records of *O. inflatus* and *O. keraudrenii.*

Family Carinariidae de Blainville, 1818
Cardiapoda placenta Lesson, 1830

Material examined

4 specimens.

Water column stratum

6-105 m.

Distribution

Circumglobal at tropical and subtropical latitudes. Western Atlantic: United States (Florida, Texas), Mexico (Yucatan, Quintana Roo); Greater Antilles (Cuba); Gulf of Mexico (23º58´N-86º52´W, 28º27´N-87º20´W), throughout the Caribbean Sea. North-central Atlantic. Eastern Atlantic: Cape Verde Islands. Indo-Western Pacific: Kenia, China; Sumatra, Madagascar; Agulhas Bank (35º49´S-23º09´E). Eastern Pacific: Mexico (Gulf of California), Costa Rica, Colombia, Peru (Tesch, 1949; Frontier, 1963; Odé & Speers, 1967; Taylor & Berner, 1970; Abbott, 1974; Thiriot-Quiévreux, 1975; Michel & Foyo, 1976; Newman, 1990; Michel & Michel, 1991; Skoglund, 1992; Cediel-Parra et al., 1995; Aravindakshan & Stephen, 1996; Lyons, 1998; Richter & Seapy, 1999; Castellanos & Suárez-Morales, 2001; Rolán, 2005; Ayón et al., 2008; Suárez-Morales et al., 2009; Angulo-Campillo et al., 2011).

Carinaria challengeri Bonnevie, 1920

Material examined

9 specimens.

Water column stratum

45-105 m.

Distribution

Tropical-subtropical. North-central Atlantic. Eastern Atlantic: Selvagens Islands. Eastern Pacific: central to southern Mexico (Pafort-van Iersel, 1983, Skoglund, 1992; de Vera et al., 2006).

Remarks

This is the first record of this species (Fig. 2) in the western Atlantic. *Carinaria challengeri* is a small species (up to 40 mm) of body transparent, cylindrical in shape, slightly curved. It is distinguished by a pair of darkly-pigmented hemispherical structures, located on the ventral surface of the tail; Bonnevie (1920) named 'claspers' these structures and indicated to be present on mature specimens. Tentacles developed, the right one small or vestigial. Swimming fin developed, with a small sucker at its margin. Conspicuous visceral mass surrounded by a shell (Pafort-van Iersel, 1983; Richter & Seapy, 1999).

Carinaria lamarckii Blainville, 1817

Material examined

1 specimen.

Water column stratum

12-105 m.

Distribution

Circumglobal at tropical and subtropical latitudes. Western Atlantic: United States (Florida, Texas), Costa Rica; Bermuda; eastern Gulf of Mexico. North-central Atlantic. Eastern Atlantic: Senegal; Azores, Cape Verde Islands. Mediterranean Sea. Indo-Western Pacific. Eastern Pacific: Canada (50ºN), Costa Rica, Peru; Galapagos (Tesch, 1949; Odé & Speers, 1967; Taylor & Berner, 1970; Abbott, 1974; Thiriot-Quiévreux, 1975; Pafort-van Iersel, 1983; Michel & Michel, 1991; Skoglund, 1992; Blumer, 1998; Lyons, 1998; Rolán, 2005; Ayón et al., 2008; Suárez-Morales et al., 2009; Frias-Martins, 2010; Janssen, 2012; Tirado, 2012).

Remarks

Geographical records of the species correspond to *C. lamarcki* and *C. lamarckii.*

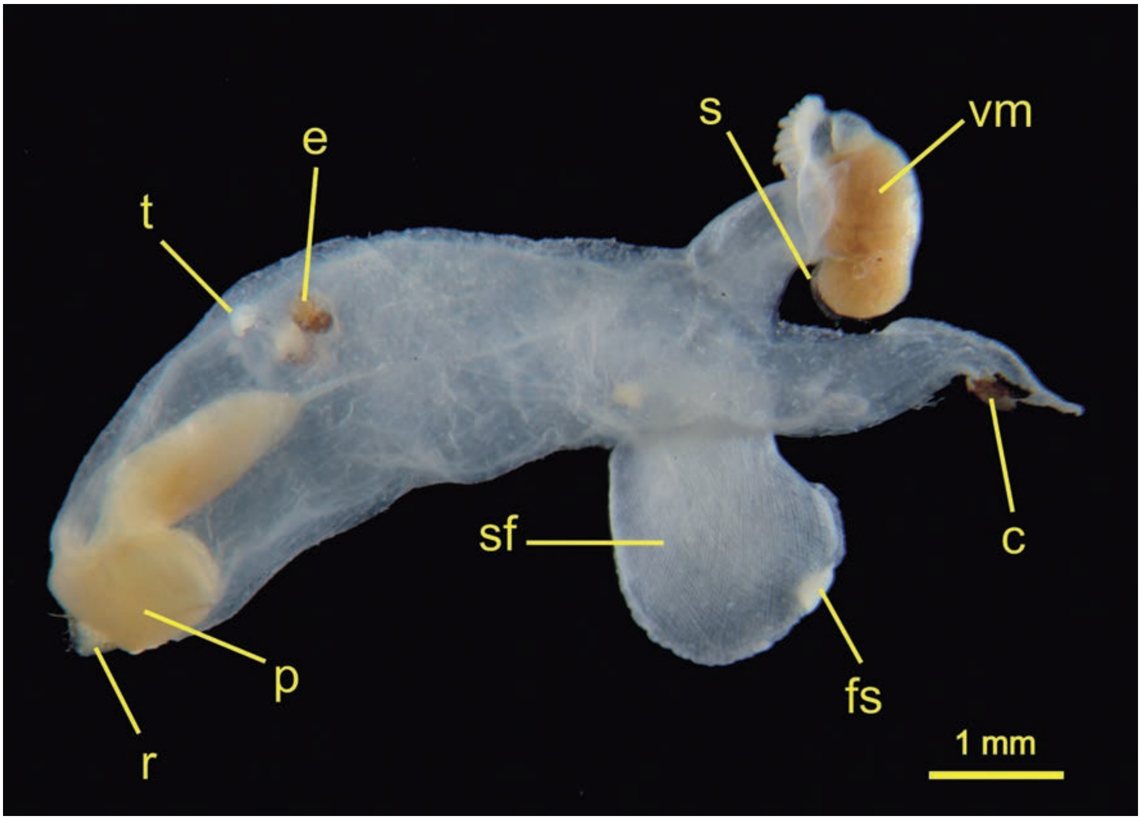

Figure 2. *Carinaria challengeri*. Lateral view of a specimen. *c*, clasper; *e*, eyes; *fs*, fin sucker; *p*, proboscis; *r*, radula; *s*, shell; *sf*, swimming fin; *t*, tentacles; *vm*, visceral mass.

Family Pterotracheidae Rafinesque, 1814
Firoloida desmarestia Lesueur, 1817

Material examined

349 specimens.

Water column stratum

0-105 m.

Distribution

Circumglobal at tropical and subtropical latitudes. Western Atlantic: United States (New Jersey, Maryland, Florida, Texas), Mexico (Veracruz, Yucatan, Quintana Roo), Colombia, Brazil; Bermuda; Greater Antilles (Cuba, Cayman, Dominican Republic); Gulf of Maine, Sargasso Sea, throughout the Gulf of Mexico. North-central Atlantic. Eastern Atlantic: Azores, Selvagens, Cape Verde Islands. Eastern Mediterranean Sea. Indo-Western Pacific: Mozambique, China; Madagascar, Australia. Central Pacific: United States (Hawaii). Eastern Pacific: United States (California), Mexico (west coast of the Baja California Peninsula, Gulf of California), Costa Rica, Ecuador, Peru, Chile; Clipperton, Galapagos (Vannucci, 1951; Owre, 1964; della-Croce & Frontier, 1966; McGowan, 1967; Odé & Speers, 1967; Fagetti, 1968; Taylor & Berner, 1970; Frontier, 1973; Abbott, 1974; Michel & Foyo, 1976; Pafort-van Iersel, 1983; Vecchione & Grant, 1983; Seapy, 1990; Skoglund, 1992; Cruz, 1996; Lyons, 1998; Richter & Seapy, 1999; Castellanos & Suárez-Morales, 2001; Pagès et al., 2001 & 2006; Seapy et al., 2003; Rolán, 2005; Çevik et al., 2006; de Vera et al., 2006; Kaiser, 2007; Xu, 2007; Ayón et al., 2008; Suárez-Morales et al., 2009; Bucklin et al., 2010; Angulo-Campillo et al., 2011; Janssen, 2012; Tirado, 2012).

Remarks

Distribution of this species was searched under the names *F. desmarestia* and *F. desmaresti*.

Pterotrachea coronata Forskål, 1775

Material examined

14 specimens.

Water column stratum

6-105 m.

Distribution

Circumglobal at tropical and subtropical latitudes. Western Atlantic: United States (Florida, Texas), Mexico (Quintana Roo), Colombia, Brazil; Gulf of Maine, throughout the Gulf of Mexico. North-central Atlantic. Eastern Atlantic: Selvagens, Canarias, Cape Verde Islands; North-eastern Atlantic (between 30 and 50°N). Mediterranean Sea. Indian Ocean: Madagascar. Central Pacific: United States (Hawaii). Eastern Pacific: Canada, United States (California), Mexico (west coast of the Baja California Peninsula, Gulf of California), Costa Rica, Peru, Chile (Dales, 1957; Frontier, 1966; McGowan, 1967; Odé & Speers, 1967; Fagetti, 1968; Taylor & Berner, 1970; Michel & Foyo, 1976; Pafort-van Iersel, 1983; Michel & Michel, 1991; Skoglund, 1992; Rios, 1994; Richter & Seapy, 1999; Castellanos & Suárez-Morales, 2001; Seapy et al., 2003; Rolán, 2005; de Vera et al., 2006; Pagès et al., 2006; Ayón et al., 2008; Oliverio, 2008; Seapy, 2008; Suárez-Morales et al., 2009; Jennings et al., 2010; Angulo-Campillo et al., 2011).

Pterotrachea hippocampus Philippi, 1836

Material examined

2 specimens.

Water column stratum

45-105 m.

Distribution

Circumglobal at tropical and subtropical latitudes. Western Atlantic: United States (Florida, Texas); Bermuda; Sargasso Sea, throughout the Gulf of Mexico. North-central Atlantic. Eastern Mediterranean Sea. Indian Ocean: Mozambique; western Australia. Central Pacific: United States (Hawaii). Eastern Pacific: United States (California), Mexico (west coast of the Baja California Peninsula, Gulf of California), Colombia, Peru, Chile (Owre, 1964; della-Croce & Frontier, 1966; McGowan, 1967; Odé & Speers, 1967; Taylor & Berner, 1970; Pafort-van Iersel, 1983; Michel & Michel, 1991; Skoglund, 1992; Cediel-Parra et al., 1995; Lyons, 1998; Richter & Seapy, 1999; Castellanos & Suárez-Morales, 2001; Pagès et al., 2001; Seapy et al., 2003; Çevik et al., 2006; Ayón et al., 2008; Oliverio, 2008; Seapy, 2008; Bucklin et al., 2010; Angulo-Campillo et al., 2011).

Discussion

Most studies concerning the heteropod fauna around the world have focused on their horizontal distribution (Frontier, 1973; Thiriot-Quiévreux, 1973; Xu, 2007). However, only few studies centered their efforts in understanding the vertical patterns of distribution (Pafort-van Iersel, 1983; Seapy, 1990 & 2008). In this study, we gave the first approach to the knowledge of the small-scale vertical distribution of the heteropod fauna collected in neritic waters of the southern Gulf of Mexico.

In general, the highest abundance of species were at the 0-18 m upper layer (Table 1), which corresponds with the highest zooplankton biomass values (Sanvicente-Añorve et al., 2013). The species *Atlanta lesueurii, A. gaudichaudi, Firoloida desmarestia* and *A. selvagensis* dominated the heteropod fauna in neritic waters of the southern Gulf of Mexico. The former three species have a circumglobal distribution at tropical and subtropical latitudes, whereas *A. selvagensis* is absent in the Pacific (Thiriot-Quiévreux, 1973; de Vera & Seapy, 2006; Janssen & Seapy, 2009). The atlantiid *A. lesueurii* largely dominated the heteropod community (Table 1). Several studies also found *A. lesueurii* to be the dominant heteropod species in oceanic waters of the Gulf of Mexico (Taylor & Berner, 1970), the East China Sea (Xu, 2007) and Hawaii (Seapy, 1990). The maximum density recorded in this study was 28 ind.100 m^{-3} (Table 1); similar results were reported for Chinese waters at comparable latitudes (Xu & Li, 2005). Seapy (1990), analysing the 0-300 m stratum of Hawaiian waters, stated that *A. lesueurii* is found from surface to 140 m depth, attaining its highest densities in the 0-50 m stratum. Our finer spatial scale study revealed that the upper stratum (0-18 m) could be their main habitat, perhaps following their prey.

Atlanta gaudichaudi was the second most abundant species (Table 1). Previous studies showed that the species is more abundant in the neritic environment, whereas in the oceanic zone it could be less abundant, as the records of the central-eastern Gulf of Mexico and Madagascar waters indicated (Taylor & Berner, 1970; Frontier, 1973). In our study area, this species was mainly found in the 0-18 m layer over the narrow shelf, area more influenced by oceanic waters. These records suggest that further studies are needed to confirm the main habitat of these organisms.

The pterotracheid *F. desmarestia* ranked third in this study. Tesch (1949) stated that this species is more numerous than the carinariids and any other pterotracheid, as our records indicated (Table 1). Taylor & Berner (1970) registered *F. desmarestia* to be the dominant species in the oceanic province of the Gulf of Mexico. In Hawaiian waters, Seapy (1990) found this species slightly more abundant in the 0-50 m layer during the day, and in the 50-100 m depth stratum at night. At a smaller spatial scale, our results indicated that the species mainly inhabit the 6-55 m layer (Table 1).

Atlanta selvagensis was the fourth most abundant heteropod species in this study (Table 1). In oceanic waters of the western Gulf of Mexico, *A. selvagensis* (as *A. inflata*) was a common species (Taylor & Berner, 1970), whereas in Atlantic oceanic waters off Panama, it was very scarce (Michel & Foyo, 1976). Our records also indicated that the species is common in the neritic zone, but possibly avoids low salinity waters (34-35). In the water column, it prefers the 0-18 m upper stratum (Table 1).

The time of reproduction in heteropods in not well known. From the four dominant species in this study, only *A. gaudichaudi* registered its highest numbers in November (Table 1). The mechanisms that originate this succession in dominance are not well understood. Some zooplankton studies signaled the ecological factors as the main force causing the shift of species dominance (de Mott, 1989). In a previous study, we did not find significant differences in zooplankton biomass (viewed as food availability) between May and November (Sanvicente-Añorve et al., 2013). Thus, we propose that shifts in seasonal dominance of heteropod species may be an adaptive strategy to avoid competition for feeding resources.

At a diel scale, results indicated that *A. lesueurii* did not show significant differences ($p > 0.05$). In accordance, Seapy (1990) did not find significant diel differences for any of the five strata of the water column analyzed (0-300 m) in Hawaiian waters. The author reported a similar pattern for *A. selvagensis* (as *A. inflata*), which partially corresponds with our findings, since we found the species more abundant at night in November, and no density differences in May. Seapy (1990) also observed no day/night differences for *F. desmarestia*; this fact strongly contrasts with our observations in the southern Gulf of Mexico, where the species were more abundant during the daytime in the upper 0-18 m layer in both months (Table 2). All these findings suggest that further field studies under different environmental conditions are needed to understand the diel vertical movements of heteropods.

Ten species registered less than 1% of the total abundance each (Table 1). Density of Carinariidae and Pterotracheidae species here encountered had the same order of magnitude as Castellanos & Suárez-Morales (2001) previously observed in the study area. Seapy (1990) suggests that these specimens are able to avoid capture; instead, Lalli & Gilmer (1989) argued that their predatory habits are the cause of their low numbers. We think that reproductive behavior is also an important factor explaining low heteropod densities. In any case, numbers were insufficient to explain their horizontal or vertical patterns in the studied area.

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